

# Microhabitat selection varies by sex and age class in the endangered green and golden bell frog *Litoria aurea*

Valdez, J.\*, Klop-Toker, K., Stockwell, M.P., Clulow, S., Clulow, J., and Mahony, M.J.

School of Environmental and Life Sciences, University of Newcastle, University Drive, Callaghan, 2308 New South Wales, Australia

\* corresponding author: E-mail: jose.valdez@uon.edu.au

## ABSTRACT

Although amphibians are one of the most threatened animal groups, little published evidence exists on effective management programs. In order for conservation initiatives to be successful, an understanding of habitat use patterns is required to identify important environmental features. However, habitat use may differ between the different sexes and age classes due to different behavioural and resource requirements. For this study, we compared microhabitat use during the active breeding season among the sexes and age classes in the endangered green and golden bell frog *Litoria aurea*, a species which has had several failed management programs. We found aquatic vegetation was selected for by every *L. aurea* class, and should be the focus of future management plans for this species. Females were the only class to select for terrestrial vegetation more than availability. Increasing the amount of terrestrial vegetation around ponds may help encourage female occupancy, and possibly improve management outcomes, as they are typically a limiting resource. Although large rock piles have been used in past *L. aurea* habitat management, they were selected for by adults and juveniles, but not metamorphs. Therefore, large rocks may not be necessary for captive breeding portions of management initiatives, which typically only involve tadpoles and metamorphs prior to release. The results indicate that the most appropriate management plans should contain a habitat mosaic of various microhabitats, such as a large proportion of aquatic and terrestrial vegetation with patches of bare ground and a small proportion of rocks for basking and shelter. Recognizing differences in microhabitat use patterns between individuals in a population and implementing them into management strategies should be a pivotal step in any conservation plan.

**Key words:** age class; amphibian; gender; habitat use; *Litoria aurea*; management; microhabitat; sex

DOI: <https://doi.org/10.7882/AZ.2016.031>

## Introduction

The current global biodiversity crisis has heightened the need for effective management of threatened species. For conservation initiatives to be successful, an understanding of habitat use patterns is required to determine how species are affected by natural and human-driven environmental changes (Mao *et al.* 2005; Sawyer *et al.* 2006; Wilson *et al.* 2016). These insights may help to build a basis for optimal decision-making and management strategies (Chetkiewicz *et al.* 2006; Kowal *et al.* 2014; Steen *et al.* 2014). A common method used by ecologists when making habitat assessments is to identify important habitat features for the species through a comparison of habitat use with its availability (Johnson 1980). However, it is unlikely that a particular habitat type will be uniformly used by a given species across its range. The favourability of habitat features are likely to vary depending on factors such as predation risk (Heithaus and Dill 2002; Mao *et al.* 2005), conspecific attraction (Pizzatto *et al.* 2015), preference toward natal habitat features (Stamps and Swaisgood 2007), disease (Threlfall *et al.* 2008), season

(Pratt and Smokorowski 2003; Zengeya *et al.* 2014), loss of natural habitat (Brand and Snodgrass 2010), food availability (Heithaus and Dill 2002), population density (Erős *et al.* 2005), and anthropogenic activities (Grindal and Brigham 1999; Mattson *et al.* 1987). By identifying variabilities in habitat use we can increase our understanding of the functional aspects of species habitat ecology and implement these features in future conservation management strategies.

Within a population, habitat preferences may also differ due to individual behavioural and resource requirements. Habitat use studies typically examine the species as a whole, without subdivision into life stages or sex classes (Barton *et al.* 1992; Furlonger *et al.* 1987; Medellín and Equihua 1998; Peña *et al.* 2015; Tew *et al.* 2000; Williams-Guillén *et al.* 2006). Although populations typically face a trade-off between survival and condition to maximize fitness, different requirements between males and females can result in differences in how the sexes

interact in their environment. Differences in habitat use between the sexes have been found in animals such as western barbastelle bats, *Barbastella barbastellus* (Hillen *et al.* 2011); American kestrel, *Falco sparverius* (Ardia and Bildstein 1997); ruffed grouse, *Bonasa umbellus* (Whitaker *et al.* 2006); tawny owls, *Strix aluco* (Sunde and M. Redpath 2006), red kangaroos, *Macropus rufus* (Johnson and Bayliss 1981); aphid parasites, *Diaeretiella rapae* (Read *et al.* 1970); and western toads, *Bufo boreas* (Bartelt *et al.* 2004; Bull 2006). Some of these differences in habitat use have been attributed to the different response by the sexes to density affects, such as in the yellowfin sole, *Limanda aspera* (Bartolino *et al.* 2010); breeding season differences, as found in the Alaskan moose, *Alces alces gigas* (Oehlers *et al.* 2011); and to human hunting, such as in wild boars, *Sus scrofa* (Said *et al.* 2012). Habitat requirements are also likely to differ substantially between earlier and later stages of life. Differences among life stages in habitat use have been reported in marsupials (Johnson and Bayliss 1981), birds (Whitaker *et al.* 2006), fish (Sempereski and Gaudin 1995), turtles (Arthur *et al.* 2008), and amphibians (González-Bernal *et al.* 2015; Searcy *et al.* 2013).

It is therefore essential to understand not just how a population uses available habitat, but also how habitat is used at the microhabitat scale by individuals to fully recognize any differences between the sex and life stages. This is exemplified by habitat use studies that focus on only one gender (Clark *et al.* 1993; Dunn and Braun 1986) or life stage (Harrel *et al.* 1996; Muhlfeld and Marotz 2005), which if the results are generalized to describe the species as a whole, may result in wrong assumptions about habitat requirements. Consequently, if differences in microhabitat preferences aren't considered, the success of interventions such as

habitat creation, rehabilitation, and habitat management for threatened species may be severely limited.

Difficulties in establishing successful habitat interventions have been observed in many animal species, most notably in amphibians. Amphibians are one of the most globally threatened animal group (IUCN 2012; Vié *et al.* 2009), highly sensitive to environmental changes, and are essential components in many ecological communities (Blaustein and Wake 1995; Blaustein *et al.* 1994; Semlitsch 2002; Vos and Chardon 1998; Wyman 1990). Due to their high conservation priority, small size, high fecundity, and minimal resources required, they are considered a model candidate for conservation programs (McFadden *et al.* 2008). However, little published evidence exists for successful management, with only 13 of the 110 programs reported in the literature having resulted in a self-sustaining population (Griffiths and Pavajeau 2008). Although research has been conducted on the general habitat requirements of threatened amphibians (Baldwin *et al.* 2006; Graeter *et al.* 2008; Laurila 1998; Wassens *et al.* 2010; Williams *et al.* 2012) and their microhabitat preferences (Blomquist and Hunter 2010; Garnham *et al.* 2015; Hamer *et al.* 2003; Heard *et al.* 2008; Hossack *et al.* 2009; Seebacher and Alford 2002; Smits 1984), the failure rate of establishing self-sustaining populations remains high. These failures indicate that inadequate background research has been carried out on the threats, life history, behaviour, as well as the habitat requirements of these species. Successful conservation outcomes may be improved not only by removing and dealing with the original or persisting key threatening processes, but also through better understanding of their habitat requirements, especially in amphibians which have complex biphasic life cycles.

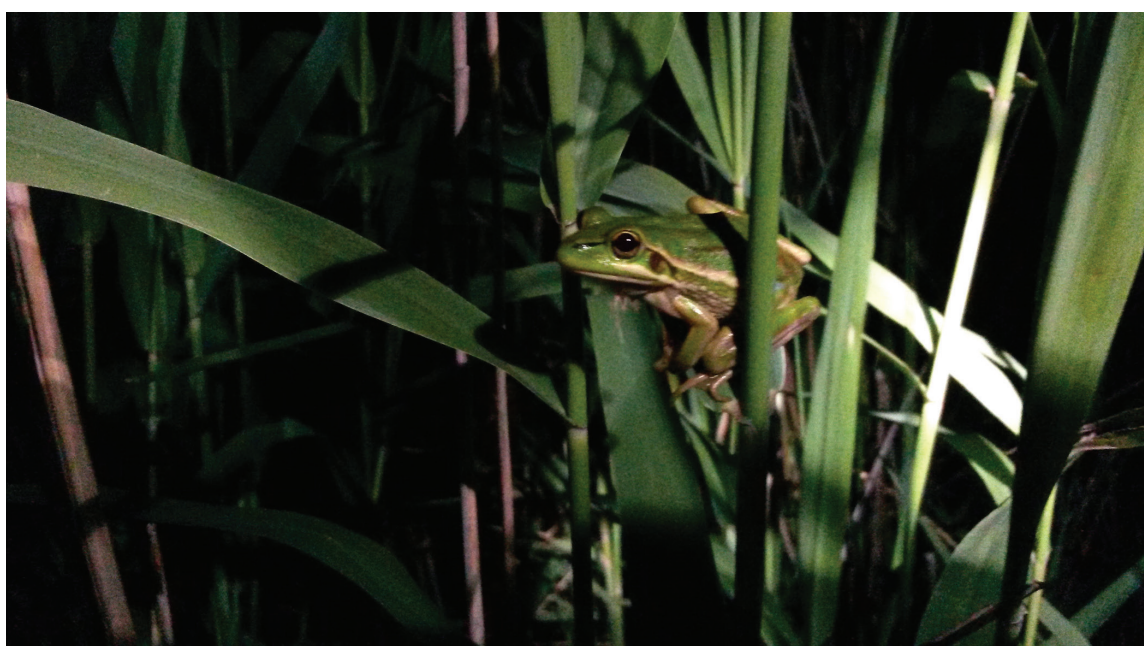


Figure 1. An adult green and golden bell frog, *Litoria aurea* on aquatic vegetation, *Typha orientalis*. Photo: Jose Valdez.



The green and golden bell frog *Litoria aurea* is one species faced with many of these conservation challenges (Fig. 1). This Australian species has undergone disease and habitat disturbance driven declines since the 1970s (Goldingay 2008; Mahony *et al.* 2013; White and Pyke 2008b). Due to its frequency of occurrence in areas of high development activity, it has had the most conservation management proposals of any Australian amphibian (Germano *et al.* 2015). As a colonizing and generalist species, *L. aurea* should be an ideal candidate for producing successful conservation programs. However, despite the use of habitat templates based on perceived microhabitat selection paradigms, nearly all habitat creation and reintroduction plans have been unsuccessful in producing a self-sustaining breeding population (Daly *et al.* 2008; Pyke *et al.* 2008; Stockwell *et al.* 2008; White and Pyke 2008a). To date, the most successful habitat creation program to result in a self-sustaining population has been at Sydney Olympic Park. This project required considerable financial input resulting in a 19-fold increase in available frog habitat (Darcovich and O'Meara 2008; O'Meara and Darcovich 2015; Pickett *et al.* 2013), and may have increased its success due to the presence of an established resident population that were able to colonise the newly-created habitat areas created nearby. Recognizing the microhabitat needs of the

sexes and life stages may help to understand the habitat components that confer survival in their remaining sites, help improve future captive breeding and habitat creation/restoration programs, as well as shed light on previous *L. aurea* habitat research.

In this study, we examined microhabitat use to availability in one of the last remaining extant population of *L. aurea* in the Hunter River Valley. The objective was to determine whether *L. aurea* actively select for and use microhabitat features similarly between the sexes and life stages. By comparing microhabitat selection between sex and age classes, we hoped to determine what microhabitat features are being used by the different classes to better inform future management programs.

## Methods

### Study site

The study was conducted across Kooragang Island which is located in the Hunter River estuary of New South Wales, Australia (-32°51'48.5634, 151°44'29.3634) (Fig. 2). This area represents one of the last remaining and largest extant *L. aurea* populations in the region (Hamer and Mahony 2010). The island is a heterogeneous estuarine landscape containing a





range of habitats including wet pasture, salt marsh, remnant forest, mangrove, and freshwater wetlands (Day *et al.* 1999). It has a history of extensive land clearing and hydrological alterations for agricultural and industrial development (Hamer and Mahony 2010). The northern half of the island is reclaimed and part of the Hunter Wetlands National Park, while the southern half is highly industrialized with waste dump sites, industrial rail loops, and coal loading facilities for the Port of Newcastle (Hamer and Mahony 2010).

### Field methods

Monthly surveys were conducted on Kooragang Island during the breeding season (September–April, inclusive) for a three-year period from April 2011 to April 2014, throughout 58 ponds (size range = 31 m<sup>2</sup> to 250,332 m<sup>2</sup>, average = 8,094 m<sup>2</sup>) (Fig. 2). Standardized visual encounter surveys (VES) involved nocturnal searches for *L. aurea* within ponds, aquatic vegetation, and surrounding terrestrial microhabitat within 1 m of the edge of the waterbody (Fig. 3) (Bower *et al.* 2014; Crump and Scott 1994). All microhabitat features were inspected and any individuals that were encountered were captured by hand using a disposable plastic bag to prevent disease transmission. The location and microhabitat type of all

individuals detected were recorded. Surveys were timed with no overlap between searchers and determined to be finished when all areas were thoroughly searched.

All frogs captured were processed by measuring their snout to vent length (SVL) and body weight (Fig. 4). We determined the sex and age class of all individuals based on secondary sexual characteristics. Individuals with an SVL of less than 45 mm were recorded as metamorphs if they had a tail with developed front and hind limbs, or as juveniles if they had resorbed their tail. Frogs larger than 45 mm were recorded as males if nuptial pads were present and as females if nuptial pads were absent (Hamer 1998). After individuals were weighed and measured they were released back at the site of capture.

Habitat availability among surveyed ponds on Kooragang Island was measured annually using quadrat-based stratified sampling methods (Krebs 1999). The landscape was stratified within the waterbodies and the pond edge, with microhabitat recorded as a proportion of the total area. Habitat features were divided into groups (see Table 1. Functional groups and descriptions of the available microhabitat used in occupied ponds by



**Figure 3.** Examples of waterbodies nocturnally surveyed across Kooragang Island, including aquatic and terrestrial vegetation, rocks, and open water microhabitats. Photo: Jose Valdez.



**Figure 4.** A female green and golden bell frog, *Litoria aurea*, about to be weighed, measured and microchipped. Photo: Jose Valdez.

the green and golden bell frogs *Litoria aurea* between April 2011 and April 2014 on Kooragang Island.) for ease of analysis.

### Data Analysis

Chi-square analysis was used to determine differences in microhabitat use between *L. aurea* classes (males, females, juveniles and metamorphs). Availability of microhabitats for each class was determined by the total percentage cover of microhabitats in the ponds where frogs of that class were found. The expected number of *L. aurea* for each class was found by multiplying the proportion of available microhabitats for the class by the

total number of individuals found in the class. To account for differences in detectability between microhabitats, an adjusted count was obtained by dividing the observed number of individuals found in each microhabitat by the probability of *L. aurea* detection for that microhabitat (Valdez *et al.* unpublished data). Chi-square values were then calculated by comparing the adjusted number of individuals found in each microhabitat with the expected number given the proportion of microhabitat availability. If a microhabitat was used more than expected it would be assumed to be preferred as a resource. This study design assumed that detectability within microhabitats did not differ between classes.

### Results

A total of 964 observations were made during the surveys between 2011 and 2014. These included 294 males, 300 females, 329 juveniles, and 41 metamorphs among the different ponds on Kooragang Island (Figure 5).

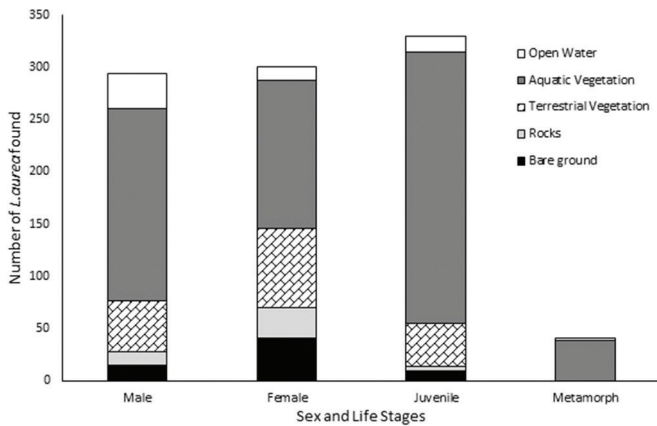
The frequency of observed microhabitat use differed between classes from the frequency expected for bare ground ( $\chi^2=336.8$ ,  $p<0.001$ ), rocks ( $\chi^2=209.17$ ,  $p<0.001$ ), terrestrial vegetation ( $\chi^2=36.9$ ,  $p<0.001$ ), aquatic vegetation ( $\chi^2=429.2$ ,  $p<0.001$ ), and water ( $\chi^2=415.7$ ,  $p<0.001$ ). After incorporating probability of detection, microhabitats were not used in the same proportion as was expected for males ( $\chi^2=257$ ,  $p<0.001$ ), females ( $\chi^2=1615.9$ ,  $p<0.001$ ), juveniles ( $\chi^2=377.1$ ,  $p<0.001$ ), and metamorphs ( $\chi^2=61.7$ ,  $p<0.001$ ).

Bare ground was used more than expected by males ( $\chi^2=103.7$ ,  $p<0.001$ ), females ( $\chi^2=1083.2$ ,  $p<0.001$ ), and juveniles ( $\chi^2=90.8$ ,  $p<0.001$ ), but used as expected by metamorphs ( $\chi^2=0.2$ ,  $p=0.65$ ) (Figure 6a). Rocks were used more than expected by males ( $\chi^2=46.2$ ,  $p<0.001$ ), females ( $\chi^2=284.4$ ,  $p<0.001$ ), and juveniles ( $\chi^2=2.5$ ,  $p=0.11$ ) but as expected for metamorphs ( $\chi^2=0.5$ ,  $p=0.49$ ) (Figure 6b). Terrestrial vegetation was used more than expected by females ( $\chi^2=15.6$ ,  $p<0.001$ ); less than

**Table 1.** Functional groups and descriptions of the available microhabitat used in occupied ponds by the green and golden bell frogs, *Litoria aurea* between April 2011 and April 2014 on Kooragang Island.

Microhabitat	Description	Example
Aquatic vegetation	Aquatic vegetation inside or around the margin of ponds	<i>Baumea articulata</i> , <i>Schoenoplectus validus</i> , <i>Typha orientalis</i> , <i>Bolboschoenus</i> spp., <i>Juncus</i> spp., <i>Schoenus</i> sp., <i>Azolla</i> sp., and other submerged plants and algae species
Terrestrial vegetation	Vegetation occurring outside but not inside a pond	Shrubs ( <i>Acacia</i> spp.), trees ( <i>Casuarina</i> spp., <i>Eucalyptus</i> spp.), grass ( <i>Kikuyu</i> , <i>Trifolium</i> spp.)
Rock	Hard substrate with a large grain size (>10 cm)	Large rocks, bricks, or other similar substrates
Bare ground	Substrate with small grain size (<10 cm) with little to no cover	Open dirt ground, mud, or leaf litter
Open water	Open water without aquatic vegetation	Open water



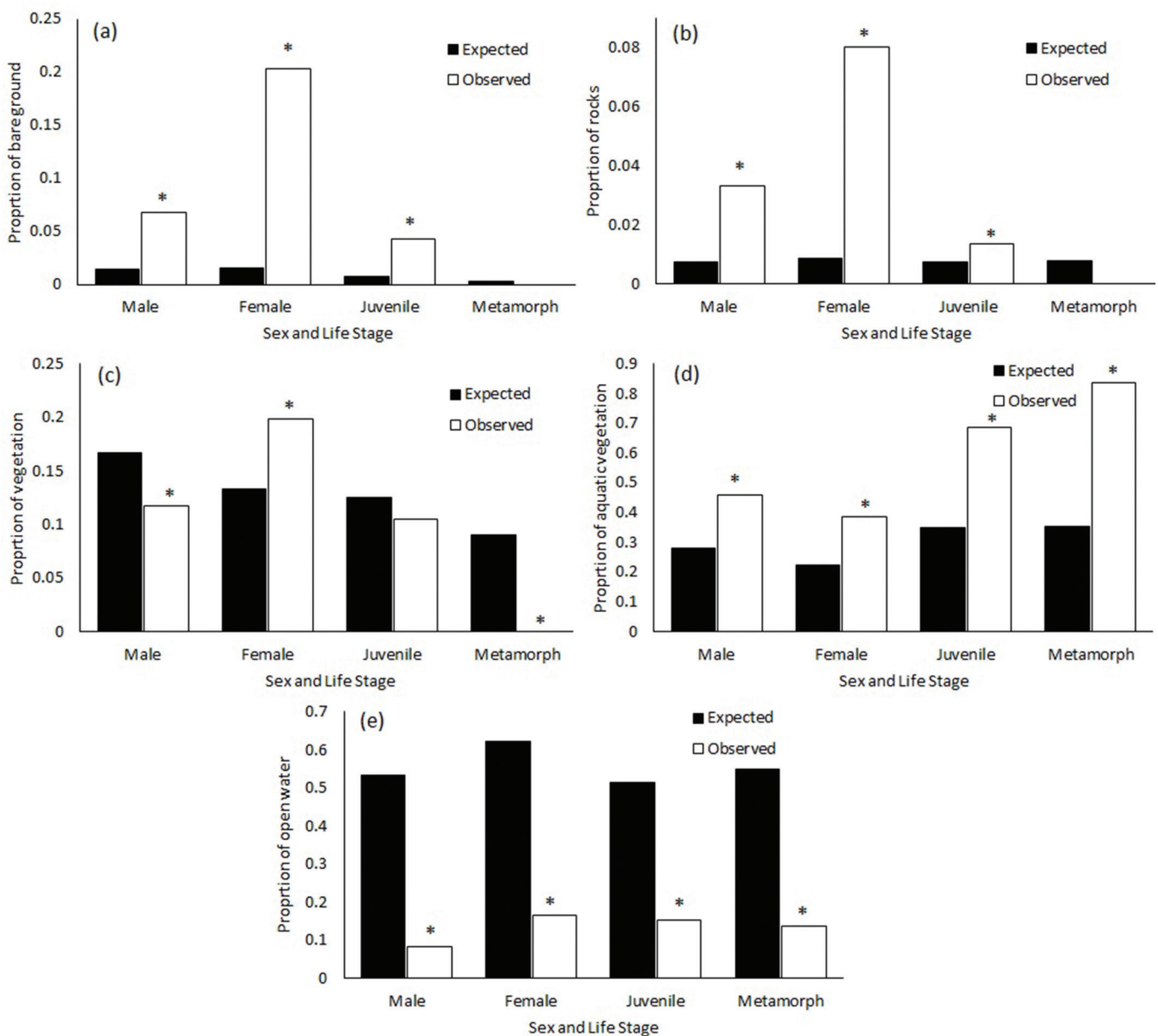


**Figure 5.** Total number of green and golden bell frogs *Litoria aurea* observed in different microhabitat types across Kooragang Island, New South Wales, Australia.

expected for males ( $\chi^2=7.33$ ,  $p<0.001$ ), and metamorphs ( $\chi^2=5.4$ ,  $p=0.02$ ); and as expected for juveniles ( $\chi^2=1.59$ ,  $p=0.21$ ), (Figure 6c). Aquatic vegetation was used more than expected by every class: males ( $\chi^2=57.9$ ,  $p<0.001$ ), females ( $\chi^2=53.9$ ,  $p<0.001$ ), juveniles ( $\chi^2=159.4$ ,  $p<0.001$ ), and metamorphs ( $\chi^2=39.7$ ,  $p<0.001$ ) (Figure 6d). Open water was used less than expected by all *L. aurea* classes; males ( $\chi^2=41.8$ ,  $p<0.001$ ), females ( $\chi^2=178.9$ ,  $p<0.001$ ), juveniles ( $\chi^2=122.8$ ,  $p<0.001$ ), and metamorphs ( $\chi^2=16$ ,  $p<0.001$ ) (Figure 6e).

## Discussion

The results indicate there were differences in microhabitat use between the different sex and age *L. aurea* classes



**Figure 6.** Proportion of observations of green and golden bell frogs (*Litoria aurea*) expected and observed, after accounting for detectability, for each sex and age class on Kooragang Island for (a) bare ground, (b) rocks, (c) vegetation, (d) aquatic vegetation, and (e) open water microhabitats. Asterisks represent significance ( $p<0.05$ ) of Chi-square test.

during the active breeding season, and which may have management implications for attracting and supporting different individuals to particular areas. For example, female *L. aurea* appear to be the limiting resource in populations (Pickett *et al.* 2015), mainly due to the relatively long time to reach sexual maturity (Mahony *et al.* 2013), coupled with the low survival rate due to the impact of the amphibian disease chytridiomycosis (Stockwell *et al.* 2010; Stockwell *et al.* 2008). As they were the only class to actively select for terrestrial vegetation, female occupancy may be encouraged by increasing the amount of terrestrial vegetation surrounding waterbodies. Terrestrial vegetation is also crucial for juveniles as it provides protection from predation and conspecifics as they actively disperse to colonize new sites (Goldingay and Lewis 1999; van de Mortel and Goldingay 1998). Moreover, since sub-adults (metamorphs and juveniles) have a low survival rate, we recommend they be released onto sites with a large area of aquatic vegetation to provide opportunities for foraging while also offering protection from predation. Large rock piles have also been widely used in past *L. aurea* management due to their recommendation in habitat guidelines produced by government conservation agencies (Pyke and White 1996). However, they were only selected for by adults and juveniles in this study, but at a very low frequency. Therefore, it may not be an important microhabitat for parts of conservation programs that only deal with tadpoles, metamorphs, and juveniles; such as captive-breeding programs prior to release.

The most important microhabitat selected by every *L. aurea* class was aquatic vegetation. These results concurs with previous studies (Garnham *et al.* 2015; Hamer *et al.* 2002) and should be the focus in all future management programs, as previously suggested (Goldingay and Lewis 1999; Pyke and White 1996). Aquatic vegetation such as submerged, emergent, and fringing plants provide critical breeding microhabitats for this species by providing oviposition sites for adults and shelter for tadpoles (Hamer and McDonnell 2008; van de Mortel and Goldingay 1998). It also serves as an important microhabitat for adults and juveniles which utilize it to forage, bask, and as shelter (Pyke and White 2001). Moreover, aquatic vegetation offers protection from predators, which is important for all age and sex classes (Goldingay and Lewis 1999; Goldingay 2008). This microhabitat is especially important for metamorphs, which require to be near water and may be particularly vulnerable to desiccation; as well as for chorusing males, whose calls may attract predators (Pyke and White 2001).

Conversely, open water was used less than expected by all class groups. Although all life stages require aquatic resources, being in open water makes them vulnerable to predators; especially if other microhabitats that provide shelter are not available (Pyke and White 2001). Actively swimming or floating in open water would likely also use more energy, whereas on aquatic vegetation they

can remain at rest in the water while still able to obtain foraging opportunities. However, breeding events such as amplexus were not observed in this study, which may have biased the outcomes. Previous research has reported that adult *L. aurea* males float on the surface of open water to actively chorus (Courtice and Grigg 1975; Thomson *et al.* 1996). Similar to other amphibian species with explosive breeding patterns (Daly 2014; Wells 1977), males have also been observed actively moving towards disturbances on the surface of open water (Ford 1986), presumably to seek opportunities with females or deter males from occupying their territorial space (Mahony, pers. comm.). Furthermore, ponds with open water would be expected to have higher water temperature, which could also influence spawning on many amphibian species (Hamer and Parris 2011). Therefore, future *L. aurea* research should focus on understanding how microhabitats are used during chorusing and reproduction.

Individuals from all classes, except metamorphs, were found on bare ground more than expected. Juveniles and adults may use bare ground to facilitate their sit and wait foraging behaviour (Heard *et al.* 2008), and although bare ground does not provide much protection against predators, it would allow a quick retreat into the water to evade them, assuming bare ground was within jumping proximity to the water (Heard *et al.* 2008). Bare ground is also important as it is commonly used for basking (Pyke and White 2001) which allows them to increase their body temperature allowing for better digestion and maximal growth (Hamer *et al.* 2003). Furthermore, *L. aurea* is known to occasionally overwinter in wet ground close to the water's edge (Garnham *et al.* 2015). Metamorphs were found less often on bare ground than predicted possibly due to their greater reliance on available water. In addition, metamorphs have restricted mobility making them an easier target for predators in open ground.

Terrestrial vegetation was used more than expected by females and less than expected by males and metamorphs. A previous study on female western toads, *Bufo boreas* also found females used vegetated areas more than males (Bartelt *et al.* 2004). This discrepancy is hypothesized to be due to the larger size of females. A larger body has a larger capacity to hold water and thus a reduced risk of dehydration, which would allow them to disperse to new sites through drier areas (Bartelt *et al.* 2004). These sex differences also occur in *L. aurea* with females larger than males (Pyke and White 2001). Males in this species also showing greater site fidelity, especially during the breeding season when males aggregate to chorus (Pyke and White 2001) and females travel to these ponds due to conspecific attraction (James *et al.* 2015; Pizzatto *et al.* 2015). Although metamorphs can be found in fringing grass and sedges (van de Mortel and Goldingay 1998), they may have been found in terrestrial microhabitats less than expected because of their site fidelity and their apparent inability to disperse. However, terrestrial

habitat is important when they become juvenile frogs and require cover when they actively disperse toward new ponds (Bower *et al.* 2013; Pyke and White 2001).

Rocks were used more than expected by adults and juveniles but not metamorphs. Rock piles, and other large solid substrates with crevices, may be selected for by *L. aurea* to bask and to provide protection from predators and unsuitable weather due to the stable microclimate and lower temperature variability in the small spaces between them (Garnham *et al.* 2015; Hamer *et al.* 2003). Similar results have been documented in another tree frog (*Bokermannohyla saxicola*), and have been hypothesized to help reduce predation by visually oriented predators (Sazima and Eterovick 2000). Since metamorphs require a greater reliance on water and are more likely to be preyed upon, the benefits of being in the open may not outweigh the risks.

Since many conservation projects on amphibians involve captive-breeding and their subsequent translocation to natural or semi-natural landscapes, the findings of the current study may improve survival of reintroduced individuals in future studies. The most appropriate plan should contain a mosaic of microhabitat types such as aquatic and terrestrial vegetation with patches of bare ground and a small proportion of large rocks. Previous research on this species on Kooragang Island indicate that a diversity of vegetation around the banks of waterbodies, such as *Juncus kraussii*, *Schoenoplectus litoralis*, and *Sporobolus virginicus* may encourage *L. aurea* presence (Hamer *et al.* 2002). Furthermore, while large rock piles have been utilized greatly in almost all past *L. aurea* habitat creation projects to provide for shelter and overwintering sites, placing large rocks as a management tool is expensive and time consuming. Reintroduction and habitat creation plans may which focus on

researching cheaper alternatives, such as vegetation mounds which has recently been hypothesized to provide shelter (White and Pyke 2015). However, caution should be taken since the hardness of rocks and similar substances may be better at providing protection from climate and predators. Lastly, even if habitat is created to the best specification, a landscape approach is required due to their colonizing ability (Valdez *et al.* 2015) and their ability to disperse over long distances after translocation releases (Stamps and Swaisgood 2007). Therefore, any successful *L. aurea* habitat creation and reintroduction management plans should include nearby permanent waterbodies in their initiatives.

Habitat creation/restoration, reintroductions, and translocation projects are emerging as pivotal methods of species conservation management. Recognizing the differences in habitat use patterns between individuals within populations may give conservation managers useful information for to make informed decisions. By taking these differences into account and incorporating them into future management strategies, it may increase the chances of success in habitat creation or enhancement programmes.

## Acknowledgements

We would like to thank the numerous volunteers that assisted with data collection. We would also like to thank Kim Colyvas for statistical help, John Gould for editing, and Port Waratah Coal Service and Newcastle Coal Infrastructure group for site access. This work was done under National Parks and Wildlife Scientific License no. SL100421, approved by the University of Newcastle Animal Care and Ethics Committee project no. A-2011-137, and funded by BHP Billiton Grant no. G1000939.

## References

- Ardia, D. R., Bildstein, K. L. 1997. Sex-related differences in habitat selection in wintering American kestrels, *Falco sparverius*. *Animal Behaviour* 53: 1305-1311. <http://dx.doi.org/http://dx.doi.org/10.1006/anbe.1996.0364>
- Arthur, K. E., Boyle, M. C., Limpus, C. J. 2008. Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. *Marine Ecology Progress Series* 362: 303-311
- Baldwin, R. E., Calhoun, A. J. K., deMaynadier, P. G. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the Wood Frog *Rana sylvatica*. *Journal of herpetology* 40: 442-453
- Bartelt, P. E., Peterson, C. R., Klaver, R. W. 2004. Sexual differences in the post-breeding movements and habitats selected by western toads (*Bufo boreas*) in southeastern Idaho. *Herpetologica* 60: 455-467. <http://dx.doi.org/10.1655/01-50>
- Bartolino, V., Ciannelli, L., Bacheler, N. M., Chan, K.-S. 2010. Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. *Ecology* 92: 189-200. <http://dx.doi.org/10.1890/09-1129.1>
- Barton, R., Whiten, A., Strum, S., Byrne, R., Simpson, A. 1992. Habitat use and resource availability in baboons. *Animal Behaviour* 43: 831-844
- Blaustein, A. R., Wake, D. B. 1995. The puzzle of declining amphibian populations. *Scientific American* 272: 52-57
- Blaustein, A. R., Wake, D. B., Sousa, W. P. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8: 60-71



- Blomquist, S. M., Hunter, M. L. 2010. A Multi-Scale Assessment of Amphibian Habitat Selection: Wood Frog Response to Timber Harvesting. *Ecoscience* 17: 251-264. <http://dx.doi.org/10.2980/17-3-3316>
- Bower, D. S., Pickett, E. J., Stockwell, M. P., Pollard, C. J., Garnham, J. I., Sanders, M. R., Clulow, J., Mahony, M. J. 2014. Evaluating monitoring methods to guide adaptive management of a threatened amphibian (*Litoria aurea*). *Ecology and Evolution* 4: 1361-1368. <http://dx.doi.org/10.1002/ece3.980>
- Bower, D. S., Stockwell, M. P., Pollard, C. J., Pickett, E. J., Garnham, J. I., Clulow, J., Mahony, M. J. 2013. Life stage specific variation in the occupancy of ponds by *Litoria aurea*, a threatened amphibian. *Austral Ecology* 38: 543-547
- Brand, A. B., Snodgrass, J. W. 2010. Value of Artificial Habitats for Amphibian Reproduction in Altered Landscapes. *Conservation Biology* 24: 295-301. <http://dx.doi.org/10.1111/j.1523-1739.2009.01301.x>
- Bull, E. L. 2006. Sexual differences in the ecology and habitat selection of Western Toads (*Bufo boreas*) in northeastern Oregon. *Herpetological Conservation and Biology* 1: 27-38
- Chetkiewicz, C.-L. B., St. Clair, C. C., Boyce, M. S. 2006. Corridors for conservation: integrating pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 37: 317-342
- Clark, J. D., Dunn, J. E., Smith, K. G. 1993. A Multivariate Model of Female Black Bear Habitat Use for a Geographic Information System. *The Journal of wildlife management* 57: 519-526. <http://dx.doi.org/10.2307/3809276>
- Courtice, G. P., Grigg, G. C. 1975. A taxonomic revision of the *Litoria aurea* complex (Anura: Hylidae) in south-eastern Australia. *Australian Zoologist* 18: 149-163
- Crump, M. L., Scott, N. J. J. 1994. Visual encounter surveys. Pp. 84-91 in *Measuring and Monitoring Biological Diversity - Standard Methods for Amphibians*. edited by W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek and M. S. Foster. Smithsonian Institution Press: London
- Daly, G. 2014. From rags to riches and back again: fluctuations in the Green and Golden Bell Frog *Litoria aurea* population at Nowra on the south coast of New South Wales. *Australian Zoologist* 37: 157-172. <http://dx.doi.org/10.7882/AZ.2014.027>
- Daly, G., Johnson, P., Malolakis, G., Hyatt, A., Pietsch, R. 2008. Reintroduction of the green and golden bell frog *Litoria aurea* to Pambula on the south coast of New South Wales. *Australian Zoologist* 34: 261-270
- Darcovich, K., O'Meara, J. 2008. An Olympic legacy: green and golden bell frog conservation at Sydney Olympic Park 1993-2006. *Australian Zoologist* 34: 236-248
- Day, S., Streever, W. J., Watts, J. J. 1999. An Experimental Assessment of Slag as a Substrate for Mangrove Rehabilitation. *Restoration Ecology* 7: 139-144. <http://dx.doi.org/10.1046/j.1526-100X.1999.72004.x>
- Dunn, P. O., Braun, C. E. 1986. Summer Habitat Use by Adult Female and Juvenile Sage Grouse. *The Journal of wildlife management* 50: 228-235. <http://dx.doi.org/10.2307/3801903>
- Erős, T., Sevcsik, A., Tóth, B. 2005. Abundance and night-time habitat use patterns of Ponto-Caspian gobiid species (*Pisces, Gobiidae*) in the littoral zone of the River Danube, Hungary. *Journal of Applied Ichthyology* 21: 350-357
- Ford, M. A. 1986. Some observations of reproductive behaviour in captive smooth-backed green frogs (*Litoria aurea*). *Tane* 31: 113-120
- Furlonger, C. L., Dewar, H. J., Fenton, M. B. 1987. Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology* 65: 284-288. <http://dx.doi.org/10.1139/z87-044>
- Garnham, J. I., Stockwell, M. P., Pollard, C. J., Pickett, E. J., Bower, D. S., Clulow, J., Mahony, M. J. 2015. Winter microhabitat selection of a threatened pond amphibian in constructed urban wetlands. *Austral Ecology* 40: 816-826
- Germano, J. M., Field, K. J., Griffiths, R. A., Clulow, S., Foster, J., Harding, G., Swaisgood, R. R. 2015. Mitigation-driven translocations: are we moving wildlife in the right direction? *Frontiers in Ecology and the Environment*. <http://dx.doi.org/10.1890/140137>
- Goldingay, R., Lewis, B. 1999. Development of a conservation strategy for the Green and Golden Bell Frog *Litoria aurea* in the Illawarra Region of New South Wales. *Australian Zoologist* 31: 376-387
- Goldingay, R. L. 2008. Conservation of the endangered green and golden bell frog; what contribution has ecological research made since 1996. *Australian Zoologist* 34: 334-39
- González-Bernal, E., Brown, G. P., Crowther, M. S., Shine, R. 2015. Sex and age differences in habitat use by invasive cane toads (*Rhinella marina*) and a native anuran (*Cyclorana australis*) in the Australian wet-dry tropics. *Austral Ecology* 40: 953-961. <http://dx.doi.org/10.1111/aec.12279>
- Graeter, G. J., Rothermel, B. B., Gibbons, J. W. 2008. Habitat Selection and Movement of Pond-Breeding Amphibians in Experimentally Fragmented Pine Forests. *The Journal of wildlife management* 72: 473-482. <http://dx.doi.org/10.2193/2006-330>
- Griffiths, R. A., Pavajeau, L. 2008. Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology* 22: 852-861
- Grindal, S. D., Brigham, M. R. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience* 6: 25-34

- Hamer, A. 1998. Aspects of the ecology of the green and golden bell frog (*Litoria aurea*) on Kooragang Island, New South Wales, Australia. University of Newcastle, Newcastle, NSW
- Hamer, A., Mahony, M. 2010. Rapid turnover in site occupancy of a pond-breeding frog demonstrates the need for landscape-level management. *Wetlands* 30: 287-299. <http://dx.doi.org/10.1007/s13157-010-0029-7>
- Hamer, A. J., Lane, S. J., Mahony, M. J. 2002. Management of freshwater wetlands for the endangered green and golden bell frog (*Litoria aurea*): roles of habitat determinants and space. *Biological Conservation* 106: 413-424. [http://dx.doi.org/10.1016/S0006-3207\(02\)00040-X](http://dx.doi.org/10.1016/S0006-3207(02)00040-X)
- Hamer, A. J., Lane, S. J., Mahony, M. J. 2003. Retreat site selection during winter in the green and golden bell frog, *Litoria aurea* lesson. *Journal of herpetology* 37: 541-545
- Hamer, A. J., McDonnell, M. J. 2008. Amphibian ecology and conservation in the urbanising world: a review. *Biological Conservation* 141: 2432-2449
- Hamer, A. J., Parris, K. M. 2011. Local and landscape determinants of amphibian communities in urban ponds. *Ecological Applications* 21: 378-390
- Harrel, J. B., Allen, C. M., Hebert, S. J. 1996. Movements and habitat use of subadult alligator snapping turtles (*Macrochelys temminckii*) in Louisiana. *American Midland Naturalist* 135: 60-67
- Heard, G. W., Robertson, P., Scroggie, M. 2008. Microhabitat preferences of the endangered Growling Grass Frog *Litoria raniformis* in southern Victoria. *Australian Zoologist* 34: 414-425
- Heithaus, M. R., Dill, L. M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83: 480-491
- Hillen, J., Kaster, T., Pahle, J., Kiefer, A., Elle, O., Griebeler, E. M., Veith, M. 2011. Sex-Specific Habitat Selection in an Edge Habitat Specialist, the Western Barbastelle Bat. *Annales Zoologici Fennici* 48: 180-190. <http://dx.doi.org/10.5735/086.048.0306>
- Hossack, B. R., Eby, L. A., Guscio, C. G., Corn, P. S. 2009. Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. *Forest Ecology and Management* 258: 1414-1421. <http://dx.doi.org/http://dx.doi.org/10.1016/j.foreco.2009.06.043>
- IUCN (2012) Summary statistics for globally threatened species. In 'International Union for Conservation of Nature and Natural Resources. '
- James, M. S., Stockwell, M. P., Clulow, J., Clulow, S., Mahony, M. J. 2015. Investigating behaviour for conservation goals: Conspecific call playback can be used to alter amphibian distributions within ponds. *Biological Conservation* 192: 287-293
- Johnson, C., Bayliss, P. 1981. Habitat Selection by Sex, Age and Reproductive Class in the Red Kangaroo, *Macropus rufus*, in Western New South Wales. *Wildlife Research* 8: 465-474. <http://dx.doi.org/http://dx.doi.org/10.1071/WR9810465>
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71. <http://dx.doi.org/10.2307/1937156>
- Kowal, V. A., Schmolke, A., Kanagaraj, R., Bruggeman, D. 2014. Resource Selection Probability Functions for Gopher Tortoise: Providing a Management Tool Applicable Across the Species' Range. *Environmental Management* 53: 594-605
- Krebs, C. J. 1999. *Ecological Methodology*. First Edition edn. Harper Collins: New York.
- Laurila, A. 1998. Breeding habitat selection and larval performance of two anurans in freshwater rock-pools. *Ecography* 21: 484-494. <http://dx.doi.org/10.1111/j.1600-0587.1998.tb00440.x>
- Mahony, M. J., Hamer, A. J., et al. 2013. Setting conservation and research priorities for endangered species in the face of uncertainty: a case study using bell frogs in eastern Australia. *Herpetological Conservation and Biology* 8: 519-538
- Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., Merrill, E. H., Hudson 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *The Journal of wildlife management* 69: 1691-1707. [http://dx.doi.org/10.2193/0022-541X\(2005\)69\[1691:HSBEBA\]2.0.CO;2](http://dx.doi.org/10.2193/0022-541X(2005)69[1691:HSBEBA]2.0.CO;2)
- Mattson, D. J., Knight, R. R., Blanchard, B. M. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Bears: their biology and management*: 259-273
- McFadden, M., Duffy, S., Harlow, P., Hobcroft, D., Webb, C., Ward-Fear, G. 2008. A review of the green and golden bell frog *Litoria aurea* breeding program at Taronga Zoo. *Australian Zoologist* 34: 291-296
- Medellin, R. A., Equihua, M. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. *Journal of Applied Ecology* 35: 13-23. <http://dx.doi.org/10.1046/j.1365-2664.1998.00272.x>
- Muhlfeld, C. C., Marotz, B. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* 25: 797-810
- O'Meara, J., Darcovich, K. 2015. Twelve years on: ecological restoration and rehabilitation at Sydney Olympic Park. *Ecological Management & Restoration* 16: 14-28
- Oehlers, S. A., Bowyer, R. T., Huettmann, F., Person, D. K.,

- Kessler, W. B. 2011. Sex and scale: implications for habitat selection by Alaskan moose *Alces alces gigas*. *Wildlife Biology* 17: 67-84. <http://dx.doi.org/10.2981/10-039>
- Peña, J., Fremgen, M., Connelly, J. C., Forbey, J. Is Habitat Use by Greater Sage-Grouse Proportional to Availability of Plant Morphotypes? in 2015 Undergraduate Research and Scholarship Conference, 2015, Boise State University, edited by: City.
- Pickett, E. J., Stockwell, M. P., Bower, D. S., Garnham, J. I., Pollard, C. J., Clulow, J., Mahony, M. J. 2013. Achieving no net loss in habitat offset of a threatened frog required high offset ratio and intensive monitoring. *Biological Conservation* 157: 156-162. <http://dx.doi.org/http://dx.doi.org/10.1016/j.biocon.2012.09.014>
- Pickett, E. J., Stockwell, M. P., Clulow, J., Mahony, M. J. 2015. Modelling the population viability of a threatened amphibian with a fast life-history. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 9-19. <http://dx.doi.org/10.1002/aqc.2564>
- Pizzatto, L., Stockwell, M., Clulow, S., Clulow, J., Mahony, M. 2015. Finding a place to live: conspecific attraction affects habitat selection in juvenile green and golden bell frogs. *Acta Oecologica* 19: 1-8. <http://dx.doi.org/10.1007/s10211-015-0218-8>
- Pratt, T. C., Smokorowski, K. E. 2003. Fish habitat management implications of the summer habitat use by littoral fishes in a north temperate, mesotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 286-300. <http://dx.doi.org/10.1139/f03-022>
- Pyke, G. H., Rowley, J., Shoulder, J., White, A. W. 2008. Attempted introduction of the endangered Green and Golden Bell Frog to Long Reef Golf Course: a step towards recovery. *Australian Zoologist* 34: 361-72
- Pyke, G. H., White, A. W. 1996. Habitat requirements for the green and golden bell frog *Litoria aurea* (Anura: Hylidae). *Australian Zoologist* 30: 224-232
- Pyke, G. H., White, A. W. 2001. A review of the biology of the green and golden bell frog *Litoria aurea*. *Australian Zoologist* 31: 563-598
- Read, D. P., Feeny, P. P., Root, R. B. 1970. Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). *The Canadian Entomologist* 102: 1567-1578. <http://dx.doi.org/doi:10.4039/Ent1021567-12>
- Said, S., Tolon, V., Brandt, S., Baubet, E. 2012. Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. *European Journal of Wildlife Research* 58: 107-115. <http://dx.doi.org/10.1007/s10344-011-0548-4>
- Sawyer, H., Nielson, R. M., Lindzey, E., McDonald, L. L. 2006. Winter Habitat Selection of Mule Deer before and during Development of a Natural Gas Field. *The Journal of wildlife management* 70: 396-403. <http://dx.doi.org/10.2307/3803685>
- Sazima, I., Eterovick, P. C. 2000. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. *Amphibia-Reptilia* 21: 439-461
- Searcy, C. A., Gabbai-Saldate, E., Bradley Shaffer, H. 2013. Microhabitat use and migration distance of an endangered grassland amphibian. *Biological Conservation* 158: 80-87. <http://dx.doi.org/http://dx.doi.org/10.1016/j.biocon.2012.08.033>
- Seebacher, E., Alford, R. A. 2002. Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of herpetology* 36: 69-75
- Semlitsch, R. D. 2002. Critical Elements for Biologically Based Recovery Plans of Aquatic-Breeding Amphibians. *Conservation Biology* 16: 619-629
- Sempeski, P., Gaudin, P. 1995. Habitat selection by grayling-II. Preliminary results on larval and juvenile daytime habitats. *Journal of Fish Biology* 47: 345-349. <http://dx.doi.org/10.1111/j.1095-8649.1995.tb01903.x>
- Smits, A. W. 1984. Activity patterns and thermal biology of the toad *Bufo boreas halophilus*. *Copeia* 1984: 689-696
- Stamps, J. A., Swaisgood, R. R. 2007. Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102: 392-409. <http://dx.doi.org/http://dx.doi.org/10.1016/j.applanim.2006.05.038>
- Steen, D. A., Godwin, J. C., McClure, C. J., Barbour, M. 2014. Informing management of endemic habitat specialists: Multiscale habitat selection by the Red Hills salamander. *The Journal of wildlife management* 78: 463-470
- Stockwell, M. P., Clulow, J., Mahony, M. J. 2010. Host species determines whether infection load increases beyond disease-causing thresholds following exposure to the amphibian chytrid fungus. *Animal Conservation* 13: 62-71
- Stockwell, M. P., Clulow, S., Clulow, J., Mahony, M. 2008. The impact of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* on a green and golden bell frog *Litoria aurea* reintroduction program at the hunter wetlands centre australia in the hunter region of NSW. *Australian Zoologist* 34: 379-386
- Sunde, P., M. Redpath, S. 2006. Combining information from range use and habitat selection: sex-specific spatial responses to habitat fragmentation in tawny owls *Strix aluco*. *Ecography* 29: 152-158. <http://dx.doi.org/10.1111/j.2006.0906-7590.04397.x>
- Tew, T. E., Todd, I. A., Macdonald, D. W. 2000. Arable habitat use by wood mice (*Apodemus sylvaticus*). *Journal of Zoology* 250: 305-311. <http://dx.doi.org/10.1111/j.1469-7998.2000.tb00774.x>



- Thomson, S. A., Littlejohn, M. J., Robinson, W. A., Osborne, W. S. 1996. Taxonomy of the *Litoria aurea* complex: a re-evaluation of the Southern Tableland populations of the Australian Capital Territory and New South Wales. *Australian Zoologist* 30: 158-169. <http://dx.doi.org/doi:10.7882/AZ.1996.008>
- Threlfall, C. G., Jolley, D. F., Evershed, N., Goldingay, R., Buttemer, W. A. 2008. Do green and golden bell frogs (*Litoria aurea*) occupy habitats with fungicidal properties? *Australian Zoology* 34: 350-360
- Valdez, J. W., Klop-Toker, K., Stockwell, M. P., Fardell, L., Clulow, S., Clulow, J., Mahony, M. unpublished data. Differences in microhabitat selection patterns between remnant and constructed habitats: results from a three year study.
- Valdez, J. W., Stockwell, M. P., Klop-Toker, K., Clulow, S., Clulow, J., Mahony, M. 2015. Factors driving the distribution of an endangered amphibian toward an industrial landscape in Australia. *Biological Conservation* 191: 520-528. <http://dx.doi.org/http://dx.doi.org/10.1016/j.biocon.2015.08.010>
- van de Mortel, T., Goldingay, R. 1998. Population assessment of the endangered Green and Golden Bell frog *Litoria aurea* at Port Kembla, NSW. *School of Health and Human Sciences Papers* 30: 398-404
- Vié, J. C., Hilton-Taylor, C., Stuart, S. N. 2009. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species. World Conservation Union
- Vos, C. C., Chardon, J. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* 35: 44-56
- Wassens, S., Hall, A., Osborne, W., Watts, R. J. 2010. Habitat characteristics predict occupancy patterns of the endangered amphibian *Litoria raniformis* in flow-regulated flood plain wetlands. *Austral Ecology* 35: 944-955. <http://dx.doi.org/10.1111/j.1442-9993.2010.02106.x>
- Wells, K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25: 666-693. [http://dx.doi.org/http://dx.doi.org/10.1016/0003-3472\(77\)90118-X](http://dx.doi.org/http://dx.doi.org/10.1016/0003-3472(77)90118-X)
- Whitaker, D. M., Stauffer, F., et al. 2006. Factors Affecting Habitat Use by Appalachian Ruffed Grouse. *The Journal of wildlife management* 70: 460-471. <http://dx.doi.org/10.2307/3803692>
- White, A. W., Pyke, G. H. 2008a. Frogs on the hop: translocations of Green and Golden Bell Frogs *Litoria aurea* in Greater Sydney. *Australian Zoologist* 34: 249-260
- White, A. W., Pyke, G. H. 2008b. Green and golden bell frogs in New South Wales; current status and future prospects. *Australian Zoologist* 34: 319-333
- White, A. W., Pyke, G. H. 2015. Vegetation mounds as over-winter Habitat for Green and Golden Bell frogs *Litoria aurea*. *Australian Zoologist* 37: 510-516. <http://dx.doi.org/doi:10.7882/AZ.2015.007>
- Williams-Guillén, K., McCann, C., Martínez Sánchez, J. C., Koontz, E. 2006. Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal? *Animal Conservation* 9: 331-338. <http://dx.doi.org/10.1111/j.1469-1795.2006.00042.x>
- Williams, P. J., Robb, J. R., Karns, D. R. 2012. Habitat Selection by Crawfish Frogs (*Lithobates areolatus*) in a Large Mixed Grassland/Forest Habitat. *Journal of herpetology* 46: 682-688. <http://dx.doi.org/10.1670/11-144>
- Wilson, R. R., Regehr, E. V., Rode, K. D., St Martin, M. 2016. Invariant polar bear habitat selection during a period of sea ice loss. *Proc. R. Soc. B.* 283
- Wyman, R. L. 1990. What's happening to the amphibians? *Conservation Biology* 4: 350-352
- Zengeya, F. M., Murwira, A., De Garine-Wichatitsky, M. 2014. Seasonal habitat selection and space use by a semi-free range herbivore in a heterogeneous savanna landscape. *Austral Ecology* 39: 722-731. <http://dx.doi.org/10.1111/aec.12137>